Effects of experimental fire regimes on the abundance and diversity of cursorial arachnids of Brazilian savannah (cerrado biome)

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Abstract. We investigated the influence of burning frequency and timing on the abundance and diversity of cursorial arachnids in the cerrado (savannah of central Brazil). Five areas were subjected to different burning regimes. In each area, 40 pitfall traps were installed. The arachnids were sampled for three days each month from April 2007 to October 2008. Abundance was higher in the control area than in areas subjected to any fire regime. Species richness was similar in all areas. The evenness was lower in the control area. The areas subject to fires had significantly higher diversity than the control area. Although it was not possible to rank areas according to their diversity, areas burned in the middle of the dry season tended to have higher diversity than areas burned at the beginning or end of this season, indicating that the time at which fire occurs may be more important than the frequency of burning for the diversity of cursorial arachnids in the Brazilian cerrado.

Keywords: Fire effects, spiders, Arachnida, Araneae

Cerrado is savannah typical of central Brazil. It covers around two million km² and includes various types of vegetation, a mix of woody and herbaceous plants. Following the Amazon Forest, it is the largest Brazilian biome and has a well-defined climate with a strong dry season during the winter (approximately May to September).

Fire is the most prevalent form of disturbance in the cerrado biome, which dates back to at least 32,000 years (Salgado-Labouriau & Ferraz-Vicentini 1994). Burning stimulates regrowth, seed germination, flowering and fruiting of many species (Miranda et al. 2002). The rapid occupation of the cerrado has increased fire frequency, threatening the biodiversity in many locations (Klink & Machado 2005).

In the cerrado, as well as in other savannahs, burns are superficial, and their effects are related to water content, according to the shade of the herbaceous layer. Small areas can be preserved from the fire, changing the landscape into mosaics of different post-burn ages and different floristic structures, and this kind of abiotic disturbance may affect the diversity patterns (Coutinho 1990; Pianka 1992; Miranda et al. 1993; Kauffman et al. 1994; Castro & Kauffman 1998; Miranda et al. 2002).

The basic premise of the Intermediate Disturbance Hypothesis is that the highest diversity is maintained at intermediate levels of disturbance on various scales of frequency and intensity by preventing competitively dominant species from excluding others (Connell 1978). Although there is variation in the response of invertebrate fauna to fire, the trend for most groups is high resilience to disturbance, the frequency being more important than the intensity of the fire (Andersen & Müller 2000).

In 1989, a long-term experiment (the "Fire Project") was initiated in a cerrado area of central Brazil, with the overall objective of determining the effects of different regimes of prescribed burning on the structure and function of this biome (Nardoto et al. 2006). Using these experimental areas, this study aimed to investigate the influence of frequency and timing of burning on abundance and the diversity of cursorial arachnids of the cerrado.

METHODS

Study site and sampling design.—This study was carried out in the Roncador Ecological Reserve (RECOR) (15°56'21"S, 47°53'07"W), Brasília, Brazil, which covers ca 1.350 ha. We used pitfall traps installed in five experimental areas (each 200 m × 500 m) of cerrado sensu stricto (excluding very open areas and gallery forests) subjected to different burning regimes (timing and frequency); 1) the control area (CT) was preserved from fire for at least 36 yr; 2) the early biennial (EB) was burned every 2 yr in early dry season (late June), similar to the occurrence of natural fires (Ramos-Neto & Pivello 2000); 3) the modal biennial (MB) was burned in the middle of the dry season (early August), a period in which anthropogenic burning is more common (Coutinho 1982; Coutinho 1990); 4) the late biennial (LB) was burned at the end of September, a period that favors the renewal of leaves and flowering of most woody plants (Oliveira & Gibbs 2000); 5) the modal quadrennial (QD) was burned every 4 yr in the middle of the dry season (early August), a period that favors the recruitment of woody biomass and the replenishment of lost nutrients (Pivello & Coutinho 1992; Kauffman et al. 1994). The last time a quadrennial plot was burned was in August 2007, while the biennial plots were last burned in July, August or September 2008.

In each plot, ten sets of traps were installed, each set consisting of four containers (35 cm diam × 45 cm depth) buried with their rim at ground level. Each container connected with others by drift fences (6 m long × 0.4 m high) in a "Y" shape. The arachnids were sampled for three days each month from April 2007 to October 2008. This experimental design followed a standardized protocol originally designed for herpetological research.

All individuals were collected alive and then conserved in 80% ethanol. The arachnids were identified to species level when possible. Voucher specimens of each spider species are deposited at the arachnid collection of the Zoology Department of the Universidade de Brasilia.

Data analysis.—Only adults were used in the statistical analysis. We used repeated ANOVA measures to investigate

Table 1.—Species list and number of individuals of cursorial arachnids (Araneae, Opiliones and Scorpiones) collected in the five experimental treatments of cerrado sensu stricto in central Brazil.

	Treatment					
Species	CT	EB	MB	LB	QD	Total
Anyphaenidae						
Aysha sp.	0	0	0	1	0	1
Barychelidae						
Neodiplothele sp. 1	0	1	7	1	5	14
Neodiplothele sp. 2	2	4	10	10	9	35
Sasoninae sp.	1	0	0	0	0	1
Caponiidae						
Caponina notabilis (Mello-Leitão 1939)	0	0	0	1	0	1
Nops sp.	3	2	0	1	2	8
Corinnidae						
Abapeba rioclaro Bonaldo 2000	2	10	12	2	12	38
Castianeira sp.	8	3	0	0	0	11
Corina capito (Lucas 1856)	1	12	10	1	10	34
Corinnidae sp. 1	5	6	5	1	2	19
Corinnidae sp. 2	16	3	0 2	3 5	2	24 11
Falconina gracilis (Keyserling 1891) Mazax sp.	1 2	2	0	0	1	2
Paradiestus giganteus (Karsch 1880)	0	3	1	4	2	10
Xeropigo camilae De Souza & Bonaldo 2007	3	3	3	0	3	12
Xeropigo tridentiger (O. Pickard-Cambridge 1869)	17	2	5	4	8	36
Ctenidae						
Calocteninae sp.	0	0	1	0	0	1
Isoctenus coxalis (F.O. Pickard-Cambridge 1902)	i	5	2	2	0	10
Isoctenus sp.	19	1	0	0	0	20
Parabatinga brevipes (Keyserling 1891)	93	30	31	24	34	212
Phoneutria eickstedtae Martins & Bertani 2007	0	1	1	1	1	4
Deinopidae						
Deinopis sp.	1	0	0	0	0	1
Dipluridae						
Diplura sp. 1	2	4	6	11	6	29
Diplura sp. 2	1	22	9	4	6	42
Ischnothele annulata Tullgren 1905	5	0	3	0	0	8
Gnaphosidae						
Apopyllus silvestrii (Simon 1905)	26	74	68	24	30	222
Apopyllus sp. 1	2	2	0	0	1	5
Camillina sp.	23	3	7	1	1	35 50
Eilica modesta Keyserling 1891 Eilica rufithorax (Simon 1893)	10 0	7 0	11 1	9	13	6
	U	Ü	1	2	3	O
Lycosidae					*0	0
Aglaoctenus lagotis (Holmberg 1876)	6 1	1 5	1 9	0 2	°0 17	8 34
Alopecosa moesta (Holmberg 1876) Alopecosa sp. 1	0	4	6	4	4	18
Alopecosa sp. 1 Alopecosa sp. 2	431	0	0	0	0	431
Alopecosa sp. 3	5	7	10	8	3	33
Arctosa sp. 1	22	18	5	12	6	63
Arctosa sp. 2	71	6	12	5	11	105
Hogna gumia (Petrunkevitch 1911)	66	63	50	19	48	246
Hogna sternalis (Bertkau 1880)	6 1	11	7 8	2	10 4	36 22
Lycosa auroguttata (Keyserling 1891) Lycosa erythrognatha Lucas 1836	21	6	4	22	8	61
Lycosa inornata Blackwall 1862	1	1	2	6	9	19
Lycosa thorelli (Keyserling 1877)	1	5	11	11	11	39
Lycosinae sp. 1	26	16	25	12	12	91
Lycosinae sp. 2	0	19	10	33	30	92
Pavocosa sp.	0	6	1	2	4	13

Table 1.—Continued.

	Treatment						
Species	CT	EB	MB	LB	QD	Total	
Trochosa sp.	58	47	28	13	37	183	
Nemesiidae							
Pycnothele sp. 1	2	9	6	5	13	35	
Pycnothele sp. 2	2	8	4	11	6	31	
Pycnothele sp. 3	1	9	7	5	7	29	
Oxyopidae							
Peucetia sp. 1	11	0	0	0	0	11	
Peucetia sp. 2 Oxyopes sp.	0	1 1	1 0	0	0	2	
Hamataliwa sp.	1	0	0	0	0	1	
Palpimanidae						·	
Palpimanidae sp. 1	1	3	6	0	0	10	
Palpimanidae sp. 2	0	í	2	0	1	4	
Palpimanidae sp. 3	0	1	1	0	0	2	
hilodromidae							
Philodromidae sp. 1	10	1	0	2	0	13	
Philodromidae sp. 2	5	0	0	1	0	6	
Philodromidae sp. 3	0	0	2	0	0	2	
Philodromidae sp. 4	0	0	2	0	0	2	
cytodidae							
Scytodes itapevi Brescovit & Rheims 2000	0	0	1	0	0	1	
parassidae							
Polybetes sp.	0	0	2	0	1	3	
Quemedice enigmaticus Mello-Leitão 1942	5	0	0	1	2	8	
Quemedice piracuruca Rheims, Labarque & Ramírez 2008	0	1	0	0	0	1	
Sparassidae sp.	0	0	i	ő	1	2	
Nephilidae							
Nephila clavipes (Linnaeus 1767)	1	0	0	0	0	1	
Theraphosidae							
Acanthoscurria aff. gomesiana	8	5	6	5	9	33	
Hapalopus sp.	3	5	12	9	8	37	
Oligoxystre bolivianum (Vol 2001)	3	1	0	2	3	9	
Sickius longibulbi Soares & Camargo 1948	0	11	22	6	8	47	
Theraphosinae sp. 1 Theraphosinae sp. 2	0	4	1 2	5 0	3 2	13 5	
	1	U	2	U	2	,	
Cheridiidae	0	0			,	2	
Argyrodes sp. Euryopis sp. 1	0	0	1 2	1	1	3 6	
Euryopis sp. 2	0	2	0	0	0	2	
Latrodectus geometricus C.L. Koch 1841	1	2	1	o o	1	5	
Steatoda ancorata (Holmberg 1876)	2	0	0	4	0	6	
Steatoda diamantina Levi 1962	25	3	2	4	2	36	
Theridiidae sp. 1 Theridion sp. 1	0	1 7	0	0	0	1 7	
Theridion sp. 2	0	0	0	0	10	10	
homisidae							
Strophius sp.	3	1	0	2	0	6	
Tmarus sp. 1	0	0	0	1	0	1	
Tmarus sp. 2	1	0	0	0	0	1	
Tmarus sp. 3	0	0	0	1	1	2	
Tmarus sp. 4	1	0	0	0	0	1	
Titanoecidae							
Goeldia sp.	0	0	0	1	0	1	

Table 1.—Continued.

	Treatment					
Species	CT	EB	MB	LB	QD	Total
Trechaleidae						
Syntrechalea brasilia Carico 2008	0	0	1	0	1	2
Zodariidae						
Cybaeodamus meridionalis Lise, Ott & Rodrigues 2010	3	2	7	0	1	13
Cybaeodamus sp.	0	12	1	0	0	13
Leprolochus birabeni Mello-Leitão 1942	54	62	35	29	46	226
Opiliones						
Eusarcus aduncus (Mello-Leitão 1942)	0	2	1	1	0	4
Gryne coccineloides (Mello-Leitão 1935)	5	8	1	6	3	23
Stygnus multispinosus (Piza 1938)	2	12	7	5	1	27
Scorpiones						
Ananteris balzanii Thorell 1891	10	9	6	5	1	31
Bothriurus araguayae Vellard 1934	12	47	32	2	12	105
Tityus fasciolatus Pessoa 1935	0	9	3	1	3	16
Total	1135	671	574	387	524	3291

the effects of treatments (main factor) and month (repeated measures) on the abundance, richness, diversity and evenness (all response variables). Later, we applied a Bonferroni multiple comparison test ($\alpha \leq 0.005$) for the required number of comparisons (n=10). We identified and removed outliers from the analysis, and applied transformations (log or square root) to the distribution of data in order to comply with the assumption of homogeneity of variances when necessary (Tabachnick & Fidel 2006; Crawley 2007). These analyses were used because they take into account the temporal autocorrelations, since the experimental units were sampled repeatedly over time (Quinn & Keough 2002).

We used rarefaction based on Mao Tau values and by the nonparametric estimator Jacknife 1, using 1000 randomizations without replacements by EstimateS (Colwell 2005). The Jacknife estimators, in general, have been found to perform quite well in extrapolation of species richness with less bias, less dependence on sample size and greater precision than other estimators (Brose et al. 2003). We used the Rényi profile to measure the diversity of the arachnid community. While traditional diversity indices supply point descriptions of community structure, according to the Rényi Equation there is a continuum of possible diversity measures that equally consider both rare and abundant species (Tóthmérész 1995; Ricotta 2003). Additionally, we used Shannon-Wiener and Simpson formulas. These indices reflect different aspects of diversity: Shannon's is sensitive to rare species, whereas Simpson's is more sensitive to changes in abundance of common species (Magurran 2004). Furthermore, both these indices are widely used in ecological studies and will enable comparisons with other similar studies.

We used MANOVA and Linear Discriminant Analysis (LDA) to separate the groups based on species composition, considering only the species with more than 10 individuals. To verify the similarity in species composition between areas, we used hierarchical cluster analysis with the single linkage clustering method and Bray-Curtis distance. This method is commonly used in community studies, since it gives more

weight to abundant species (extensively sampled) in the separation of groups (Magurran 2004). The Rényi and Pielou indices, cluster analysis and the hypothesis tests were performed using the statistical program R-2.10.0 (R Development Core Team 2009) and the BiodiversityR package.

RESULTS

Sampling effort.—We collected 4,132 individuals, including 2,699 males (65%), 592 females (15%) and 849 juveniles (20%), representing 98 species (Table 1). The rarefactions based on MaoTau and Jacknife 1 values indicated that our sampling effort was suitable to collect most of arachnid species in each area (Fig. 1). The most abundant species were *Alopecosa* sp. 2, *Hogna gunia* and *Leprolochus birabeni*. Twenty-nine species (30%) were represented by fewer than five individuals (Table 1).

The fire regimes explained most (52%) of the variation in abundance values. In the control area, there were significantly more spiders captured than in LB and QD ($F_{4.18-69} = 6.2$, P < 0.001, Fig. 2). There was no significant difference in abundance between CT and EB (P = 0.71) or MB area (P = 0.35). The areas had similar richness ($F_{4.18-69} = 2.0$, P = 0.08, Figs. 1a,3).

The control area had the lowest equitability (Pielou), differing significantly from all other areas under fire regimes $(F_{4,18-69} = 3.0, P = 0.02, \text{Fig. 4})$. The areas subjected to fire individuals were more evenly distributed amongst the species.

Based on the Rényi index values, the control area had the lowest diversity in relation to experimental fire areas (Fig. 5), although the differences are only marginally significant when alpha values are equal to 4 (H_4 : 9.34, P = 0.053). Intersections of profiles (Fig. 5) indicate that the areas cannot be separated based on the community as a whole (dominant and rare species taken simultaneously).

According to the Shannon-Wiener index, the areas could be separated into three groups $(F_{4,18-69} = 18, P < 0.01)$: the first, composed of MB and QD, had the highest diversity; the second (EB and LB), had intermediate diversity; and CT had the lowest diversity. The Simpson index $(F_{4,18-69} = 13, P <$

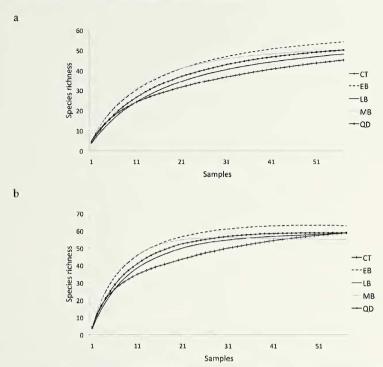


Figure 1.—Rarefaction values generated from 1000 randomizations without reposition and with a 95% confidence interval, performed in five experimental treatments of the Fire Project. a. MaoTau; b. Jacknife 1.

0.01) indicated that QD had the highest diversity, followed by MB and LB, while the treatments EB and CT presented the lowest diversity of arachnids (Table 2).

Species composition and similarity between treatments.—The treatments differed in species composition (Wilk's Lambda = 0.034, df = 4.9, P < 0.01, Fig. 6). The control area was characterized by higher abundance of Alopecosa sp. 2 and Philodromidae sp. 2.; the QD plot featured *Theridion* sp. 2, and the treatments with biennial fire (EB, MB and LB) had more *Isoctenus coxalis* and Palpimanidae sp. 1.

The hierarchical cluster analysis split the composition of the soil arachnids into two groups (Mantel r=0.97, P<0.01), one containing the control area (CT), and the other including all areas subjected to different burning regimes. Within the second group, LB area was separated from the others, which were very similar to each other in species composition (Fig. 7).

DISCUSSION

Abundance.—Slightly lower abundance in the late burning regimes (LB and QD) is consistent with the studies by Andersen et al. (2005) on the responses of cursorial Australian spiders to savannah burning and Ferrenberg et al. (2006) in American coniferous forest. Moreover, Moretti et al. (2002)

found an increase in the abundance of spiders because of a higher frequency of burning in the Swiss Alps. Several factors may explain the variation in abundance patterns presented, among which are the types of vegetation, spider guild or groups of species. Beside the differences in burning regime the differences in abundance were probably due to structural changes in the environment and not to the direct effects of fire (mortality). According to Miranda et al. (1993), savannah fires are of short duration and do not promote a significant increase in soil temperature at depths greater than five centimeters. Thus, individuals that are sheltered at the time of burning are protected from lethal temperatures promoted by fire (Ghione et al. 2007). It is noteworthy that the onset of the rainy season marks the reproductive period of most species, and fire at that time may eventually promote reductions in population, since individuals are more active and therefore more exposed to the adverse effects of fire.

Species richness.—Given the similarity in the values of richness, there is no support for the Intermediate Disturbance Hypothesis of Connell, where high richness would have been expected in the intermediate stage of disturbance in frequency (QD) or season (MB). These results agree with the pattern proposed by Mackey and Currie (2000), that richness shows

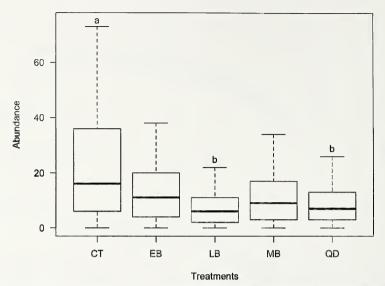


Figure 2.—Boxplot of abundance of cursorial arachnids collected in the five experimental treatments. Different letters indicate significant difference (P < 0.05) between the abundance of treatments.

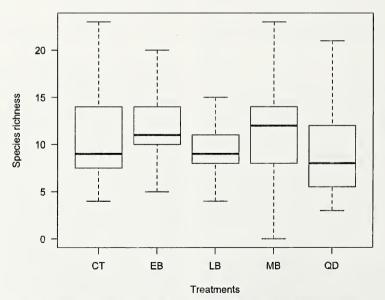


Figure 3.—Boxplot of richness of cursorial arachnids collected in the five experimental treatments.

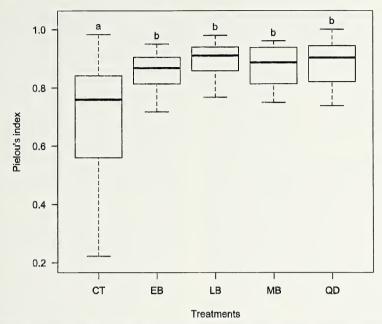


Figure 4.—Boxplot of evenness values (Pielou's J) for the species collected in the five experimental treatments. Different letters indicate significant difference (P < 0.05) between the evenness of treatments.

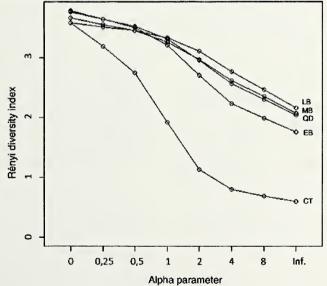


Figure 5.—Rényi diversity profiles ($\alpha = 0, ...\infty$) for the five experimental treatments.

Table 2.—Diversity values calculated from Shannon-Wiener and Simpson indices for the five experimental treatments. Different letters indicate significant difference (P < 0.001) between the treatments, using a pair-wise comparison.

	Shannon-Wiener		Simpson	
Treatment	mean ± SD		mean ± SD	
CT	2.38 ± 0.12	a	6.12 ± 0.2	a
EB	3.08 ± 0.16	b	14.8 ± 1.2	b
MB	3.22 ± 0.17	С	18.3 ± 2.1	C
LB	3.11 ± 0.21	b	17.9 ± 2.4	С
QD	3.25 ± 0.21	С	21.1 ± 2.5	d

little variation in response to environmental disturbances and to the lack of a wide gradient of disturbance.

Species composition, diversity, and evenness.—Little is known about the specific habitat of arachnids in the cerrado; however, the fact that Alopecosa sp. 2 was restricted to the CT area indicates that this species exhibits a preference for environments preserved from fire and with high densities of woody plants. In addition, Theridion sp. 2 was more abundant in the QD area, and Isoctenus coxalis and Palpimanidae sp. 1 in areas with a biennial burning regime (EB, MB and LB). The results indicate that the fire did not affect the number of species, but reduced the population size and increased the evenness, thereby promoting a greater diversity of species of cursorial arachnids. Mackey & Currie (2000) pointed out that evenness can be strongly influenced by fires, which was confirmed by this study.

However, it is not possible to corroborate the Intermediate Disturbance Hypothesis based on the results presented here, due to the impossibility of clearly ordering diversity among the areas subjected to fire. Furthermore, in contemplating a wider disturbance gradient, for example, the long time lag between the area burned every 4 yr (QD) and the area preserved for 36 yr, it is impossible to predict the diversity in areas burning often within that time frame. These results agree with Mackey and Currie (2001), who suggest that when the diversity peak is not reached in a moderate stage of disturbance this is, in most cases, due to the paucity of studies on broader levels of disturbance. This lack of methodological amplitude causes a weak correlation between diversity and moderate perturbations. Another important aspect that has not been considered is the influence of different successional stages of vegetation on the community of cursorial arachnids in the cerrado, being an important issue to be investigated in further studies.

Similarity.—The groups formed by the cluster analysis suggest two areas with different burning frequencies, but the same period (MB and QD), are very similar in composition of arachnids.

The lack of rain, while promoting the loss of fuel moisture available to burn during the dry season, influences the behavior of fire through the dry season (Miranda et al. 2002). Thus, it is expected that burning in the same season in the cerrado will modify the vegetation and litter in a similar way, therefore promoting the coexistence of spider species with similar environmental requirements.

Concluding, the areas subjected to fires presented a higher diversity than unburned areas, and burned areas in the middle of the dry season tended to have higher diversity than areas burned at the beginning or end of this season, indicating that the timing of fire may be more important than the frequency of burns on the diversity of cursorial arachnids in the Brazilian savannah (cerrado).

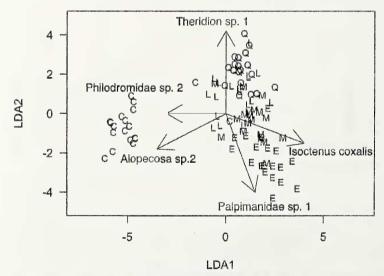


Figure 6.—Canonical variables obtained from the discriminant function generated by the distribution of cursorial spiders present in five experimental treatments.

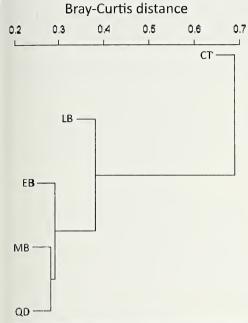


Figure 7.—Hierarchical cluster analysis based on the composition of arachnid assemblage, and with reference to the Bray-Curtis values for separation of groups.

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